

FLORAL ANATOMY OF MYRTACEAE, II. EUGENIA

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UNTIL FAIRLY RECENTLY, the floral anatomy of the Myrtaceae had been a rather neglected area of botanical research (see Schmid, 1972c, for references to earlier work, especially those cited for Carr & Carr). Recent work on the *Eugenia-Syzygium* controversy (Schmid, 1971, 1972a-c) based the recognition of both taxa on new floral anatomical as well as on hitherto unemphasized organographic evidence. The bearing of floral anatomy on the taxonomy of the strictly Old World genus *Syzygium sensu lato* was the concern of a previous report (Schmid, 1972c), whereas the comparative floral anatomy of the mainly New World *Eugenia sensu stricto* (but including, for convenience, the Old World segregate *Jossinia*) is dealt with here.

MATERIALS AND METHODS

Reproductive material of three extra-American and 20 American species (including two varieties) of *Eugenia s. s.* was examined. TABLE I lists voucher specimens and other pertinent information for the species analyzed. Detailed methodology as well as reviews of the taxonomic and anatomical literature were given in earlier papers (Schmid, 1972b, c).

TABLE I: Collection and preparation data for species studied ¹

SPECIES, LOCALITY, COLLECTOR ²	SECT. ³	CLEARED ³	
		MTD.	UNMTD.
<i>Eugenia acapulcensis</i> Steud. MEXICO: Chiapas. <i>Breedlove 14490.</i>	4	0	0
— —. MEXICO: Michoacán. <i>McVaugh 22554.</i>	4	5	0
— —. NICARAGUA: Zelaya. <i>Standley 20016.</i>	5	0	0
<i>Eugenia aeruginea</i> DC. BRITISH HONDURAS. <i>Gentle 8073.</i>	4	0	0
— —. GUATEMALA: Petén. <i>Contreras 1403.</i>	0	3	6
— —. GUATEMALA: Petén. <i>Contreras 114.</i>	0	4	0
<i>Eugenia biflora</i> (L.) DC. BRAZIL: Pará. <i>Black 52-15623.</i>	2	4	0
— —. COLOMBIA: Vaupés. <i>Schultes & Cabrera 14236.</i>	1	6	0
— —. VENEZUELA: Bolívar. <i>Steyermark & Wurdack 31.</i>	3	4	0
— —. BRAZIL: Amapá. <i>Pires & Westra 48813.</i>	3	5	0
— —, var. <i>wallenii</i> (Macf.) Krug & Urban. JAMAICA. <i>Hart 1048.</i>	4	3	0
<i>Eugenia capuli</i> (Schlecht. & Cham.) Berg. MEXICO: Chiapas. <i>Breedlove 14407.</i>	5	12	4
— —. BRITISH HONDURAS. <i>Gentle 5044.</i>	6	2	6
<i>Eugenia cartagensis</i> Berg. COSTA RICA. <i>Austin Smith 77.</i>	6	5	0
<i>Eugenia coffeifolia</i> DC. LESSER ANTILLES: Guadeloupe. <i>L'Herminier s.n.</i>	9	0	0

— —. LESSER ANTILLES: St. Lucia. <i>Proctor 17978.</i>	2	7	0
<i>Eugenia confusa</i> DC. LESSER ANTILLES: St. Lucia. <i>Proctor 18135.</i>	3	0	0
— —. JAMAICA. <i>Proctor 23563.</i>	0	7	4
<i>Eugenia duchassaingiana</i> Berg. LESSER ANTILLES: Guade- loupe. <i>L'Herminier s.n.</i>	5	1	2
<i>Eugenia flavescens</i> DC. SURINAM. <i>Florschütz & Maas</i> <i>2653.</i>	5	4	0
<i>Eugenia florida</i> DC. COLOMBIA: Amazonas. <i>Schultes &</i> <i>Cabrera 16236.</i>	6	0	0
— —. VENEZUELA: Bolívar. <i>Steyermark & Gibson</i> <i>95781.</i>	0	4	0
<i>Eugenia gregii</i> (Sw.) Poir. LESSER ANTILLES: St. Lucia. <i>Proctor 18244.</i>	5	0	0
— —. LESSER ANTILLES: Martinique. <i>Hahn 641.</i>	0	2	2
<i>Eugenia mandevillensis</i> Urban. JAMAICA. <i>Proctor 26872.</i>	2	0	1
— —. JAMAICA. <i>Proctor 19686.</i>	3	1	2
<i>Eugenia muricata</i> DC. BRAZIL: Amapá. <i>Pires et al.</i> <i>50887.</i>	7	2	2
<i>Eugenia oerstediana</i> Berg. MEXICO: San Luis Potosí. <i>King 4405.</i>	8	4	0
— —. BRITISH HONDURAS. <i>Gentle 2533.</i>	6	0	0
— —. MEXICO: Jalisco. <i>McVaugh 23418.</i>	4	5	0
<i>Eugenia pleurocarpa</i> Standl. MEXICO: Nayarit. <i>McVaugh</i> <i>15322.</i>	7	7	1
<i>Eugenia salamensis</i> Donn. Sm. var. <i>hiraefolia</i> (Standl.) McV. COSTA RICA. <i>Pittier 13952.</i>	5	0	0
— —, var. <i>salamensis</i> . MEXICO: Jalisco. <i>Carter &</i> <i>Chisaki 1209.</i>	3	4	0
<i>Eugenia tikalana</i> Lundell. GUATEMALA: Petén. <i>Con-</i> <i>treras 1116.</i>	7	7	0
<i>Eugenia uniflora</i> L. BERMUDA. <i>Taylor 49-1048.</i>	4	5	0
— —. LESSER ANTILLES: Nevis. <i>Proctor 19469.</i>	0	3	0
<i>Eugenia venezuelensis</i> Berg. GUATEMALA: Petén. <i>Con-</i> <i>treras 2971.</i>	4	5	0
<i>Eugenia whytei</i> Sprague in Stapf. LIBERIA. <i>Cooper 452.</i>	1	0	0
<i>Eugenia winzerlingii</i> Standl. GUATEMALA: Petén. <i>Con-</i> <i>treras 1619.</i>	4	0	0
— —. MEXICO: Yucatán. <i>Lundell 851.</i>	0	8	0
— —. MEXICO: Yucatán. <i>Enriquez 815.</i>	0	2	0
<i>Jossinia aherniana</i> (C. B. Rob.) Merr. PHILIPPINES. <i>Velasco s.n. (Forestry Bureau 21779).</i>	4	1	0
<i>Jossinia palumbis</i> (Merr.) Diels. MARIANA ISLANDS. <i>Hosokawa 7570.</i>	2	0	0

¹ Voucher specimen of *Jossinia aherniana* at US (specimen courtesy Dr. R. H. Eyde), all others at MICH.

² Government administrative subdivisions (e.g., state, province, department, territory, etc.) given for larger countries only.

³ Number of buds, flowers, and/or fruits sectioned (Sect.) and/or cleared. Columns under "Cleared" refer to number of items mounted (Mtd.) on permanent slides and unmounted (Unmtd.). All preparations from herbarium material.

OBSERVATIONS — GENERAL

Descriptions of the general organography, histology, and vasculature of *Eugenia s. l.* were presented in Schmid (1972b). Only the distinctive transeptal ovular supply of *Eugenia s. s.* is detailed below.

A variable number (up to about 11 per flower in my material) of bundles (placental strands) originate in several ways and constitute the transeptal ovular supply: (1) exclusively from the vascular cylinder of the floral tube (e.g., *Eugenia capuli*, FIGURE 13; *E. confusa*, FIGURE 1), (2) exclusively from a lateral carpellary system of various types (e.g., *E. flavescens*, FIGURE 18), (3) exclusively from the dorsal carpellary bundles (e.g., sometimes in *E. biflora*), or, usually (4) from any combination of the above. The mode and level of origin of the placental strands is by no means constant for a species or even an individual.

The placental strands enter the septum at different levels in the locular region and fuse variously (cf. FIGURES 3, 18, 19), eventually terminating at one or two centrally located placental plexuses. If a single placental plexus occurs, it may be a solid mass of vascular tissue (e.g., *Eugenia coffeifolia*, *E. tikalana*, *E. uniflora*, FIGURE 19) or it may be perforated by varying amounts of interfascicular parenchyma (e.g., *E. biflora*). As might be expected, these features are very variable within a species and in an individual.

There are at least three possible relationships between the dorsal carpellary bundles and the placental vascular system: (1) no connections as in *Eugenia capuli* (FIGURE 13), (2) occasional direct connections as in *E. confusa* (FIGURES 1, 3) or, usually (3) many indirect connections since a complex network of lateral carpellary bundles is interpolated between the dorsals and the placental vascular system, as in most species (e.g., *E. flavescens*, FIGURE 18). The presence or absence of an anastomosing lateral carpellary system is apparently not related to the size of the flower.

Many of these features of the transeptal ovular system are quite variable within a species or an individual. Nevertheless, it seems the ovarian vasculature of the species of *Eugenia s. s.* that I studied in detail can be broadly categorized as follows:

Dichotomous comparison of main types of ovarian vasculature in *Eugenia s. s.*

- (1) Placental strands pendulous from near tops of loculi, the placental system (including strands and plexuses) thus appearing U- or V-shaped.

Placental strands on entering septum usually massive and often two, sometimes additional slender placental strands occurring; FLORIDA-type (FIGURE 15): e.g., *E. florida*, *E. biflora*, *E. coffeifolia*, *E. gregii*, *E. oerstediana*, *E. salamensis*.

- (1) Placental strands entering sides of septum, the strands on entering septum usually slender.

- (2) Placental strands usually few, with no connections to other carpellary vasculature (dorsal or lateral bundles); dorsal bundles also not connected to other carpellary bundles; CAPULI-type (FIGURE 13): e.g., *E. capuli*, *E. venezuelensis*.
- (2) Placental strands few to many, with connections to other carpellary vasculature; dorsal bundles also connected to other carpellary bundles.
- (3) Dorsal bundles obscure; bundles to style several to often many (about 12); UNIFLORA-type (FIGURE 19): e.g., *E. uniflora*.
- (3) Dorsal bundles readily definable; bundles to style two to several (to about 6); common.
- (4) Placental strands usually few, with few connections to other carpellary vasculature, and these connections only to dorsal bundles; anastomosing carpellary system scanty or absent; CONFUSA-type (FIGURES 1, 3): e.g., *E. confusa*, *E. tikalana*.
- (4) Placental strands often many, with few to many connections to dorsal and/or to lateral carpellary bundles, both of which generally form a simple to complex anastomosing system; FLAVESCENS-type (FIGURE 18): e.g., *E. flavescens*, *E. cartagensis*, *E. winzerlingii*.

EXPLANATION OF TABLE II: Floral structure of *Eugenia* s. s. and *Jossinia*

The abbreviations at the head of each column correspond to the following taxa: Bif A, *Eugenia biflora*, Pires & Westra 48813 (MICH); Bif B, *E. biflora*, Black 52-15623 (MICH); Bif C, *E. biflora*, Schultes & Cabrera 14236 (MICH); Cap, *E. capuli*; Car, *E. cartagensis*; Cof, *E. coffeifolia*; Con, *E. confusa*; Fla, *E. flavescens*; Flo, *E. florida*; Oer, *E. oerstediana*; Sal s, *E. salamensis* var. *salamensis*; Sal h, *E. salamensis* var. *hiraeifolia*; Tik, *E. tikalana*; Uni, *E. uniflora*; Ven, *E. venezuelensis*; Win, *E. winzerlingii*; Jos, *Jossinia aherniana*.

CHARACTER 1. The maximum size of the bud near anthesis, width (at widest part of perianth) times length (base to tip of bud), was determined from sectioned or cleared material. This creates a bias toward smaller buds since these are often selected for easier manipulation and study. Maximum dimensions as indicated in the taxonomic literature are often much greater.

CHARACTER 2. The maximum prolongation of the floral tube above the ovary was determined according to taxonomic criteria. Such measurements, however, may include some ovarian tissue due to the top of the ovary being depressed (see Schmid, 1972b).

CHARACTER 5. The amount of pubescence was graded as follows: glabrous, essentially glabrous, little, or much.

CHARACTER 6. The vasculature of other floral parts is also invariably closed.

CHARACTER 7. See Schmid (1972b) for definition of terms.

CHARACTER 8. Minor bundles in some species are more or less uniformly dispersed throughout tissue of floral tube in the locular region of flower.

CHARACTER 10. The major bundles usually branch distally.

CHARACTER 11. See text for descriptions of types of ovarian vasculature.

CHARACTER 12. This includes all carpellary vasculature (except dorsal bundles) in locular region.

TABLE II. Features of floral structure of *Eugenia* s. s. and *Jossinia* *

CHARACTER	<i>Bif A</i>	<i>Bif B</i>	<i>Bif C</i>	<i>Cap</i>	<i>Car</i>	<i>Cof</i>	<i>Con</i>	<i>Fla</i>	<i>Flo</i>	<i>Oer</i>	<i>Sal s</i>	<i>Sal h</i>	<i>Tik</i>	<i>Uni</i>	<i>Ven</i>	<i>Win</i>	<i>Jos</i>
ORGANOGRAPHY																	
(1) Maximum size bud (mm. width × length)	4.0× 6.2	3.5× 5.3	1.8× 2.8	1.7× 2.2	2.3× 3.7	2.2× 3.0	2.7× 4.1	2.6× 4.5	2.5× 3.6	2.7× 3.9	3.8× 5.0	3.8× 5.2	1.6× 2.0	3.0× 5.0	1.6× 1.8	3.5× 5.0	5.4× 7.5
(2) Max FT prolonged (mm.)	.4	.5	.7	0	.25	0	.6	0	.4	.4	.2	1.1	0	.5	0	.1	1.3?
HISTOLOGY																	
(3) Scleren in flower	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(4) Scleren in pedicel	—	—	—	—	+	dna	—	—	X	—	—	—	—	+	—	+	dna
(5) Amount pubescence fl	m	m	m	li	g	li(m)	g	g	eg(m)	eg	m	m	li	g(eg)	li	g	m
VASCULATURE FT																	
(6) Vasc open or closed	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl	cl
(7) Mono- or zonocyclic	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono	mono
(8) Minor VBs diffused	—	—	—	—	—	—	—	—	+	+	—	+	—	—	—	—	+
(9) Amount minor vasc	m	m	m	li	m	li	m	m	m	m	m	m	li	m	li	m	m
(10) # MBs at base	8(9)	8	8?	8	8,10	8	8	8	8	8(9)	8	8(-10?)	8	8	8	8	8

VASCULATURE OVARY

(11) Type	flo	flo	X	cap	fla	flo	con	fla	flo	flo	flo	flo	con	uni	cap	fla	dna
(12) Amount VT by loculi	li	v li	v v li	v li	li	m	li	m	m	m	m	m	v li	m	v li	li	v v m
(13) Anastomoses in LCV	+	+	-	-	+	+	-	+	+	+	+	+	-	+	-	+	+(v m)
(14) DCBs connected to other carpellary VT	+	+	-	-	+	+	+	+	+	+	+	+	+	dna	-	+	dna

VASCULATURE STYLE

(15) # VBs at base	2(3)	2	2	2	2(3)	2	2(3)	2	3-5	3-6	2	2	2	5-12	2	3(2,4)	3-5
(16) SVBs extension of both DCBs	+	+	+	+	+	+	+	+	+	+	+	+	+	dna	+	+	dna
(17) SVBs extension of LCBs	occ	-	-	-	occ	-	occ	-	+	+	-	-	-	+	-	u	+
(18) SVBs branched	-	-	-	occ	+	occ	occ	+	u	+	+	-	-	+	-	+	+
(19) VT to tip	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	nearly	+
(20) VT at tip expanded	+	+	+	u	+	+	+	u	+	+	+	-	+	+	-	+	X

* See preceding page for explanation of characters and abbreviations of names of taxa.

SYMBOLS AND ABBREVIATIONS: The following are used, without punctuation, to shorten entries: **X**, could not be determined from my material; +, present or yes; -, absent or no; **cap**, capuli-type; **cl**, closed; **con**, confusa-type; **DCBs**, dorsal carpellary bundles; **dna**, does not apply; **eg**, essentially

glabrous; **fl**, flower; **fla**, flavescens-type; **flo**, florida-type; **FT**, floral tube; **g**, glabrous; **li**, little; **LCBs**, lateral carpellary bundles; **LCV**, lateral carpellary vasculature; **m**, many, much; **max**, maximum; **MBs**, major vascular bundles; **occ**, occasionally; **scleren**, sclerenchyma; **SVBs**, stylar vascular bundles; **u**, usually; **uni**, uniflora-type; **v**, very; **vasc**, vasculature; **VBs**, vascular bundles; **VT**, vascular tissue.

These types of ovarian vasculature are typological and do not necessarily indicate relationships since several patterns seem of general occurrence in the genus.

OBSERVATIONS — INDIVIDUAL SPECIES

Much repetitive descriptive information for the species of *Eugenia s. s.* investigated is relegated to TABLE II. Detailed descriptions are given for *E. biflora*, *E. capuli*, and *E. confusa*. Reference should be made both to the tables and to the species descriptions for a complete profile of any one species. The account for each species is based on all the specimens examined (see TABLE I) and represents a range of variability for one or more specimens (individuals) of that species.

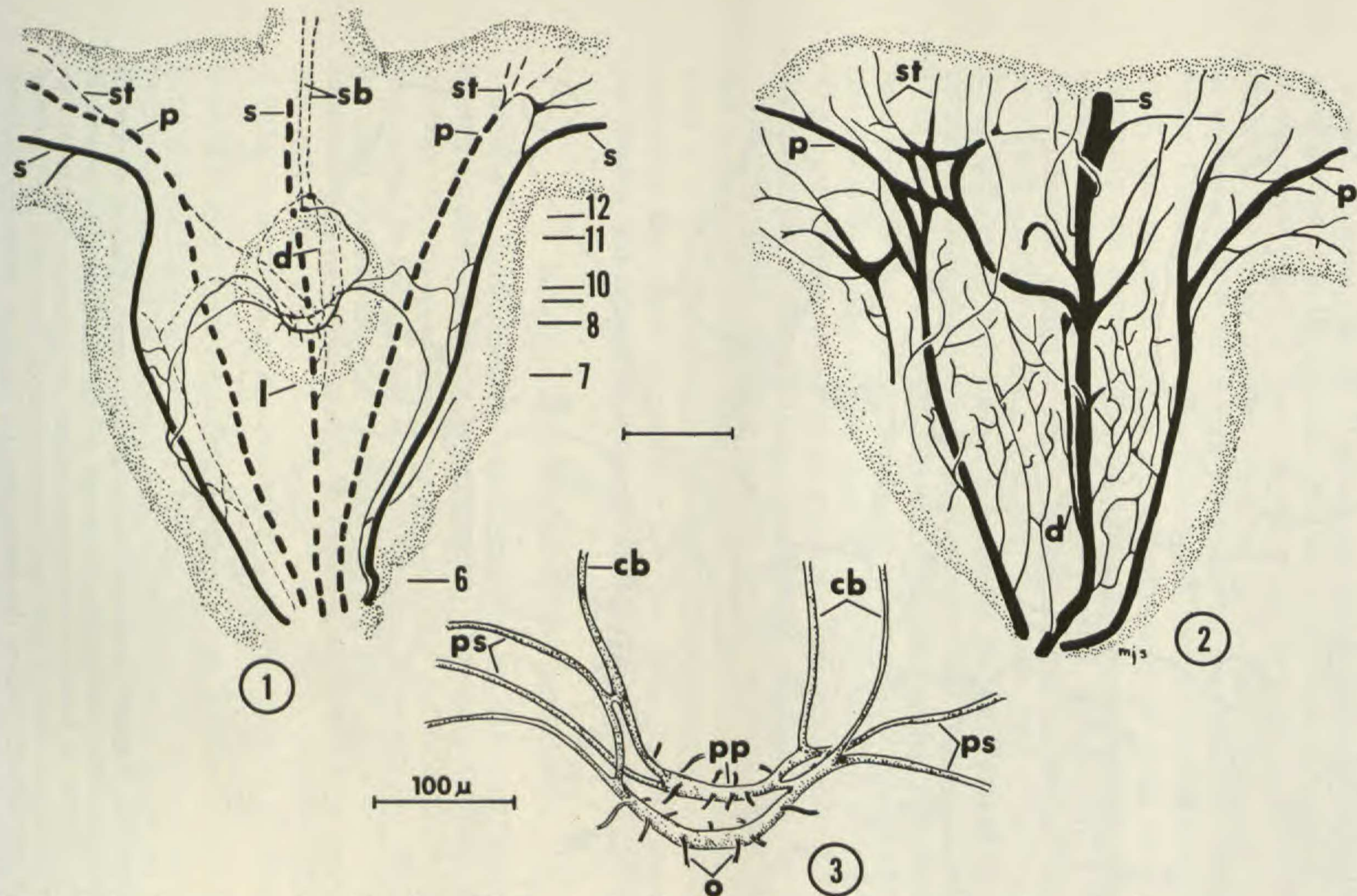
Organographic and histological data were not heavily emphasized since their apparent minor taxonomic usefulness in a small survey such as mine did not justify the labor involved in their compilation. Detailed study of a number of taxa revealed that several features of vasculature exhibit much variability. Hence, a number of vascular characters examined for *Syzygium s. l.* (see Schmid, 1972c) were not studied in detail for many species of *Eugenia s. s.* For example, the level and nature of origin of the dorsal carpellary bundles were not determined for many taxa of *Eugenia s. s.* since these features are very variable and difficult to define, much more so than in *Syzygium s. l.* (see Schmid, 1972a, c). The vascular characters given in TABLE II were selected as the most promising for comparative purposes.

The arrangement of the 13 American species examined in the greatest detail is essentially according to similarity of ovarian vasculature, based on the five types described above. Taxa were designated as exemplifying a particular type of ovarian vasculature chiefly because clearings of excellent quality were available for three-dimensional reconstructions. Comparisons between patterns of vasculature of the floral tube, ovary, and style are not necessarily indicative of relationships since several patterns seem of general occurrence in the genus (as noted above).

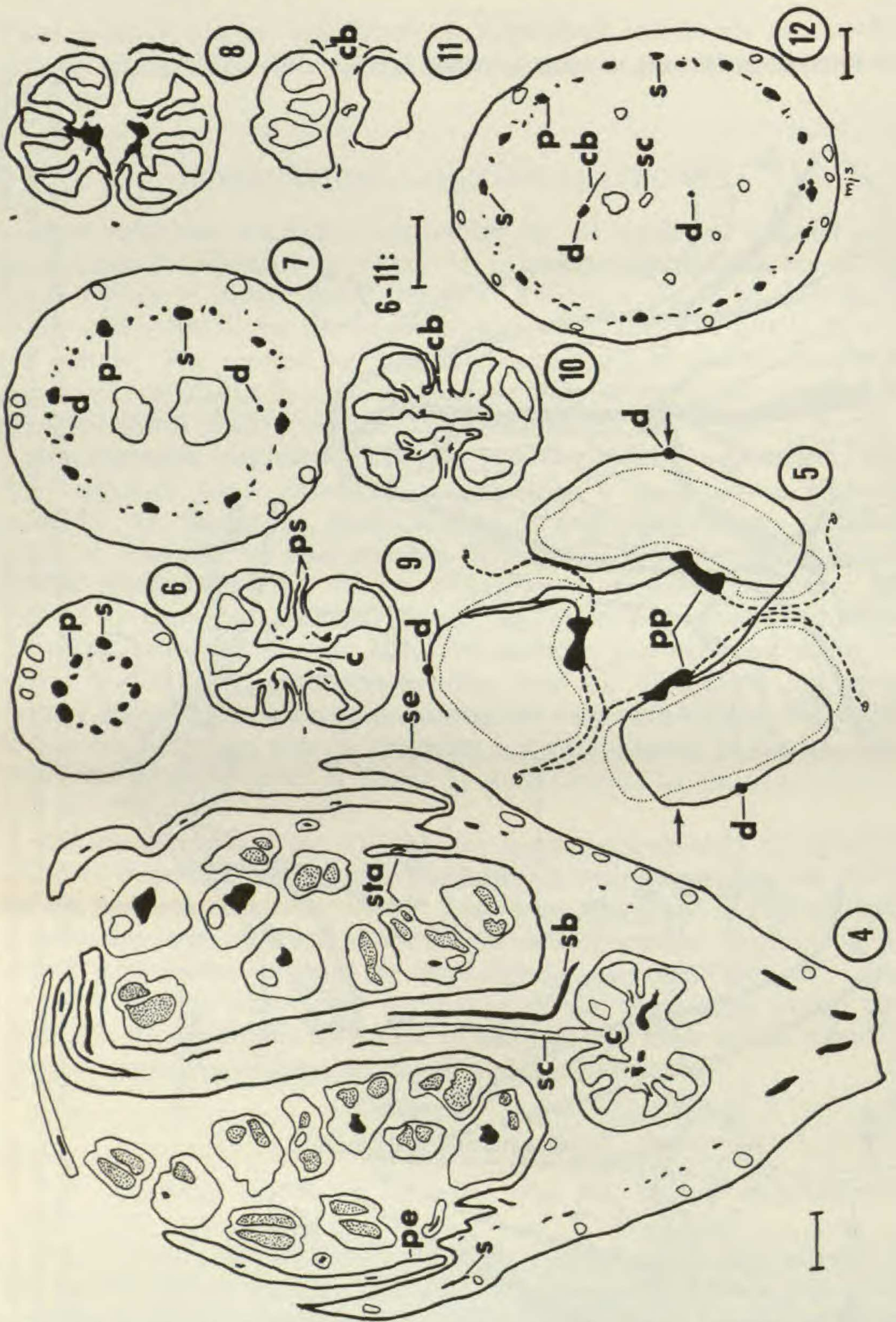
Eugenia confusa DC.

For synonymy see Urban (1895). The two plants examined are anatomically very similar.

VASCULATURE. See TABLE II. A single, unbranched bundle extends to the tip of each of the two bracteoles subtending the flower. The floral vasculature forms a closed system. Eight discrete major bundles comprise the vascular cylinder in the base of the flower (FIGURES 1, 2, 6). Throughout the extent of the floral tube, these eight bundles exhibit a monocyclic arrangement (defined in Schmid, 1972b) and frequently branch, producing mostly small minor strands that anastomose profusely in a very irregular pattern (FIGURES 2, 6, 7, 12). Distally, the eight major bundles, which usually extend into the eight perianth parts, branch extensively in an irreg-



FIGURES 1-3. *Eugenia confusa* (Proctor 23563, MICH). FIGURES 1, 2, Reconstruction of part and counterpart of a cleared flower cut in plane of septum between the two carpels. Minor vasculature omitted from FIGURE 1, vasculature of FIGURE 2 complete. Numerals at edge of FIGURE 1 indicate approximate levels of transections shown in FIGURES 6-12. FIGURE 3, Enlargement of FIGURE 1 showing placental system formed by five placental strands and three central axis bundles. ABBREVIATIONS: cb, central axis bundle; d, dorsal carpellary bundle; l, limits of ovarian locule; o, ovular trace; p, petal bundle; pp, placental plexus; ps, placental strand; s, sepal bundle; sb, stylar bundle; st, stamen trace. Unlabeled magnification bar equals 250 μ .



FIGURES 4-12. *Eugenia confusa* (Proctor 18135, MICH). FIGURE 4. Longi-section of anomalous tricarpellate flower cut in plane indicated by arrows in FIGURE 5. FIGURE 5. Transverse reconstruction of flower in FIGURE 4, representing telescoped view of placental region. Dashed lines indicate placental strands at levels mainly below the three placental plexuses; solid lines indicate central axis bundles at levels above placental plexuses. Outlines of loculi (dotted lines) correspond to level of placental plexuses; compitum and outlines of

ular manner and supply narrow traces to the stamens and generally thicker strands to the perianth segments (FIGURES 1, 2).

The ovarian vasculature exemplifies the CONFUSA-type (FIGURES 1, 3). It is complex and exceedingly variable, much more so than originally thought (Schmid, 1970). The several placental strands originate from various sources in the vascular cylinder of the floral tube, that is, directly from a major bundle or more typically from the anastomosing strands produced by the major bundles (FIGURES 1, 8). In addition, they originate at various levels in the flower, from near its base to within the placental region (FIGURE 1). As they ascend and traverse the tissue next to the loculi, the placental strands occasionally produce short branches, but eventually the former enter the middle part of the septum, turn downward, and terminate at two placental plexuses (FIGURES 1, 3, 5, 8, 9). Each placental plexus is usually formed by the fusion and subsequent proliferation of the placental strands of the same carpel (FIGURES 3, 5, 8). There is generally little contact between the placental strands of adjacent carpels, although these strands do come very close together in the septum (FIGURES 5, 8, 9). Several bundles, designated central axis bundles, extend from the four corners of the placental system and connect with the two dorsal carpellary bundles near the tops of the loculi (FIGURES 3, 5, 10-12). FIGURE 5, based on an atypically tricarpellate flower, illustrates the variability of vasculature in the placental region.

The two dorsal carpellary bundles usually originate below the loculi and occasionally produce short branches that terminate in the ovary (FIGURES 1, 2, 7). The dorsals, sometimes accompanied by a third strand, vascularize the style (FIGURES 1, 4). The stylar bundles generally do not branch, but expand near the tip of the style (FIGURES 1, 4).

Eugenia capuli (Schlecht. & Cham.) Berg

Synonyms include *Myrtus capuli* Schlecht. & Cham. and *Eugenia contrerasii* Lundell (see McVaugh, 1963a, b). The only difference detected between the two collections I studied was that the stylar bundles of one specimen (*Breedlove 14407*) were distally expanded and occasionally branched whereas those of the other (*Gentle 5044*) were not. The latter collection had been identified as *E. contrerasii* Lundell. The fact that the two collections are so very similar anatomically supports McVaugh's (1963a, b) inclusion of *E. contrerasii* in the synonymy of *E. capuli*.

loculi at other levels not indicated. FIGURES 6-12, Transections of flower taken from levels indicated in FIGURE 1. Only locular portions of flowers are shown in FIGURES 8-11 since outer vasculature is similar. FIGURE 7 is above level of origin of dorsal carpellary bundles, these omitted from FIGURES 8-11. In FIGURES 6, 7, and 12 the eight largest bundles correspond to the major bundles, four sepal bundles alternating with four petal bundles. ABBREVIATIONS: c, compitum; cb, central axis bundle; d, dorsal carpellary bundle; p, petal bundle; pe, petal; pp, placental plexus; ps, placental strand; s, sepal bundle; sb, stylar bundle; sc, stylar canal; se, sepal; sta, stamen. Magnification bars equal 250 μ .

HISTOLOGY. The floral tube and sepals are puberulent (see Schmid, 1972b, *Figures 1, 2*).

VASCULATURE. See TABLE II. A single, unbranched bundle extends to the tip of each of the two nearly contiguous bracteoles. The vasculature of the flower forms a closed system. Eight discrete major bundles occur in the tip of the pedicel and the base of the flower (FIGURE 13). In contrast to *Eugenia confusa* (FIGURE 2), these eight major bundles produce relatively few minor, anastomosing strands throughout the extent of the floral tube (FIGURE 13). Distally, the eight major bundles divide profusely in an irregular manner and supply strands to the four sepals, the four petals, or the many stamens (FIGURE 13).

The ovarian vasculature exemplifies the CAPULI-type (FIGURE 13). Originating either directly from a major bundle or generally from anastomoses produced by the major bundles, a variable number of placental strands arise at various levels in the flower and enter the ovarian tissue (FIGURE 13). At the ends of the septum, these placental strands fuse into two compound placental strands that traverse the septum. The placental vasculature usually does not exhibit the arching pattern characteristic of *Eugenia confusa*. In the center of the ovary, the two compound placental strands each divide and form two placental plexuses. The vascular tissue in the placentae thus displays a diamond-shaped pattern, with a parenchymatous core (FIGURE 13). There are no vascular connections between the placental vascular system and the dorsal carpellary bundles, unlike the situation in *E. confusa*.

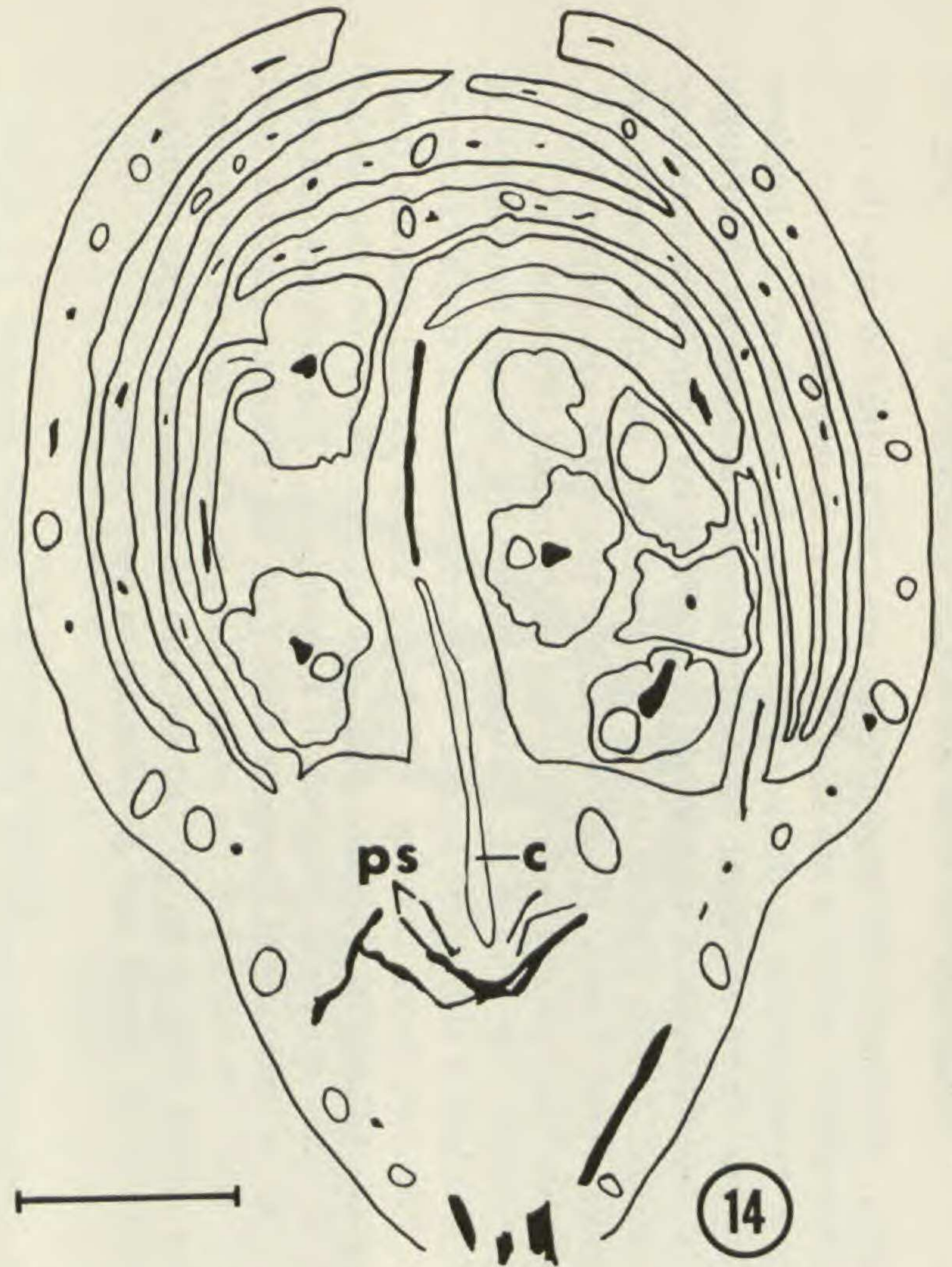
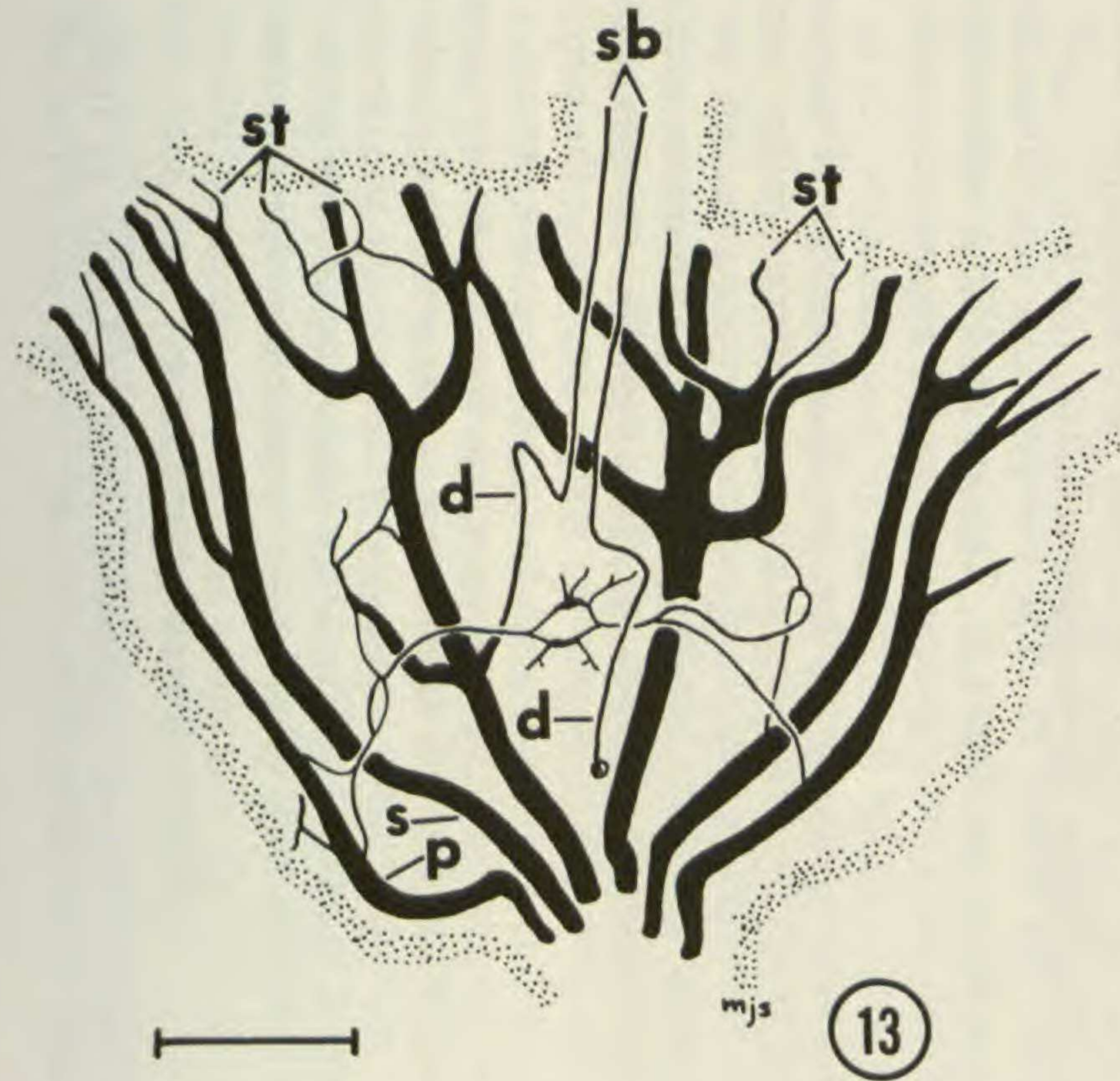
The level and manner of origin of the two dorsal bundles is very variable. The dorsals usually originate in the locular region, but they may arise anywhere from just above the loculi to near the junction of the pedicel and flower. In addition, each dorsal originates either directly from a major bundle or sometimes from several anastomosing strands produced by one or more major bundles. The dorsals do not branch in the ovary and only occasionally, distally, in the style (FIGURE 13). The bundles usually expand near the tip of the style.

Eugenia tikalana Lundell

McVaugh (1963b, p. 366) remarked that "this species is superficially almost indistinguishable from *E. capuli*." Anatomically, the two species are also very similar, *E. tikalana* differing only in its gynoecial vasculature (TABLE II, characters 11 and 14), which is of the CONFUSA-type (FIGURES 1, 3). In *E. tikalana* several placental strands enter the sides of the septum and terminate at a single placental plexus (FIGURE 14). There are usually a few vascular connections between the placental system and the dorsal carpellary bundles, as in *E. confusa*.

Eugenia venezuelensis Berg

Synonyms include *Eugenia origanoides* Berg. The name usually used is *E. origanoides* (see McVaugh, 1958, 1963a, b, for full description and



FIGURES 13 and 14. FIGURE 13, *Eugenia capuli* (*Breedlove 14407*, MICH). Reconstruction of cleared flower. Minor vasculature and part of flower with two major bundles omitted for clarity. Ovarian loculi not indicated. Four sepal bundles alternate with four petal bundles. FIGURE 14, *Eugenia tikalana*. Longisection of flower cut in plane of septum, showing central placental plexus. ABBREVIATIONS: c, compitum; d, dorsal carpellary bundle; p, petal bundle; ps, placental strand; s, sepal bundle; sb, stylar bundle; st, stamen trace. Magnification bars equal 250μ and 310μ respectively.

synonymy). However, McVaugh informs me (1971) that he saw the type of *E. venezuelensis* and it is the same as that of *E. organoides*.

Eugenia venezuelensis is distinguished from *E. capuli* or *E. tikalana* chiefly by its more abundant and conspicuous pubescence (McVaugh, 1963a, b), but the hairs of the three species are of very similar morphology (as in Schmid, 1972b, *Figures 1, 2*). Anatomically, the three species are very similar (see TABLE II) although the placental vasculature of *E. venezuelensis* more closely resembles that of *E. capuli* (FIGURE 13).

VASCULATURE. See TABLE II. At each end of the septum two placental strands fuse into a compound strand that terminates at a single placental plexus. The two stilar bundles, which end as far as 210 microns from the stigma, terminate further from the stigma than do the stilar bundles of other species of *Eugenia s. s.* examined. The delicate vascular strand (one or two vessel elements thick) of the filament expands considerably (over 10 times) in the connective and abuts against a terminal secretory cavity that is up to 110 microns in dimension. The staminal vasculature of *E. capuli* and *E. tikalana* is very similar.

Eugenia florida DC.

For synonymy see McVaugh (1958, 1969). The two collections I examined are anatomically very similar. See also remarks under *Eugenia oerstediana*.

HISTOLOGY. The sepals are ciliate (see Schmid, 1972b, *Figure 5*), and strigose chiefly within (see Schmid, 1972b, *Figures 3, 4*). One collection (*Steyermark & Gibson 95781*) has a very pubescent floral tube and staminal disc (see Schmid, 1972b, *Figures 3, 4*).

VASCULATURE. See TABLE II. The non-gynoecial vasculature is like that of *Eugenia biflora* (see TABLE II; FIGURES 16, 17). A chief difference is that in *E. florida* there are numerous tiny bundles between the loculi and the vascular cylinder of the floral tube.

The ovarian vasculature exemplifies the FLORIDA-type (FIGURE 15). Near the bottoms of the loculi many minor carpellary bundles bend inward from the innermost part of the floral tube, become arranged in a ring with the two dorsal carpellary bundles, and distally anastomose with each other and with the dorsals (FIGURE 15). Two (usually) massive placental strands originate from this anastomosing system just above the loculi and descend in opposite ends of the septum to the two placental plexuses (FIGURE 15). However, unlike other species which have the FLORIDA-type of ovarian vasculature, in *Eugenia florida* there are no additional slender placental strands entering at lower levels. Above the loculi the two dorsals and a variable number of other bundles (some containing only unligified elements) often fuse with each other before entering the style (FIGURE 15).

Eugenia oerstediana Berg

Synonyms include *Eugenia vincentina* Krug & Urban ex Urban, *E. conzattii* Standl., *E. cocquericotensis* Lundell, *E. petenensis* Lundell, and

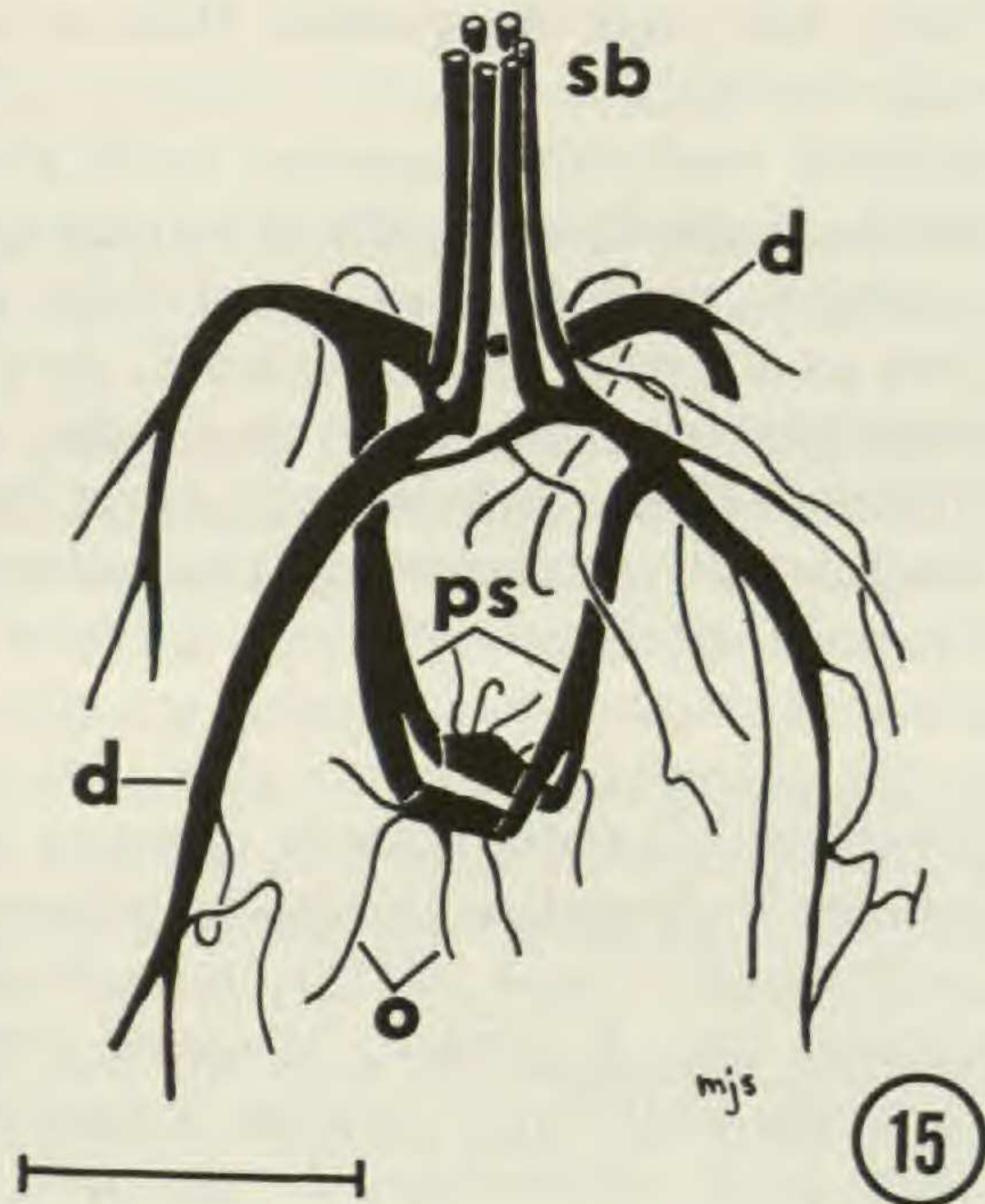


FIGURE 15. *Eugenia florida* (Steyermark & Gibson 95781, MICH). Reconstruction of placental system and associated carpellary vasculature. Two placental plexuses are present. Outlines of ovarian loculi and some minor vasculature omitted. ABBREVIATIONS: d, dorsal carpellary bundle; o, ovular trace; ps, placental strand; sb, stylar bundle. Magnification bar equals 250 μ .

E. eutenuipes Lundell (see McVaugh, 1963a, b). It should be noted that Berg's (1855-56) *E. oerstediana* is an orthographic error for *E. oerstediana*.

Of the three collections sampled, one had been identified as *Eugenia oerstediana* (McVaugh 23418), another as *E. conzattii* (King 4405), a third as *E. cocquericotensis* (Gentle 2533). McVaugh (1963a, b) considered the latter two names to be synonyms of the former. Floral anatomy supports this treatment since all three collections are very similar. Any two flowers, either from the same plant or from two different collections, may vary in a few very subtle respects, but analysis of a total of 27 flowers for the three collections indicates most such variations merely represent different points on a morphocline. Gentle 2533, however, differs slightly and consistently from the other two collections, chiefly in having (1) the dorsal carpellary bundles only weakly connected to the other carpellary bundles and (2) the two massive placental strands attached usually just below (as opposed to just above) the tops of the loculi. King 4405 differs from the other two collections in having (1) an extremely short floral tube (.1 mm. versus .3-.4 mm.), (2) very many tiny bundles occurring between the loculi and the vascular cylinder of the floral tube, and (3) the minor carpellary bundles occurring further from the loculi than do comparable carpellary bundles of the other collections. Gentle 2533 and King 4405 both differ from McVaugh 23418

in having, respectively, four and six (rather than a variable number) strands at the base of the style.

Taxonomically, *Eugenia oerstediana* appears to be closely allied to *E. florida* (McVaugh, 1963a, b, 1969) and perhaps derived from it (McVaugh, 1963a). McVaugh (1963a, p. 448) questioned "the propriety of recognizing *E. oerstediana* as a species distinct from *E. florida*" since the two are "virtually indistinguishable" except in ovule number and in characters of the inflorescence and pedicel. Anatomically, my three collections of *E. oerstediana* are exceptionally similar to my two collections of *E. florida* (see TABLE II). The only consistent difference I found between the two species is that the placental strands in *E. florida* are attached at a slightly higher level so that the placental system in side view appears more U-shaped, with nearly vertical placental strands (FIGURE 15), whereas that of *E. oerstediana* appears V-shaped, with sloping placental strands. One collection of *E. oerstediana* (McVaugh 23418), in particular, is anatomically nearly indistinguishable from *E. florida*. It seems, then, that *E. florida* is best regarded as a widely distributed complex comprised of such scarcely distinguishable forms as *E. oerstediana*, *E. conzattii*, and *E. cocqueri-cotensis*, to mention just the species for which anatomical evidence is now available.

HISTOLOGY. Only the sepals are pubescent (ciliate, with hairs like those in Schmid, 1972b, *Figure 1*).

VASCULATURE. See TABLE II. As explained above, the vasculature is very close to that of *Eugenia florida*.

Eugenia biflora (L.) DC.

McVaugh (1958, 1969) and Urban (1895) give extensive synonymy. I examined five collections for *Eugenia biflora* (see TABLE I). Since these are rather dissimilar, there are three entries for this species in TABLE II, as explained below.

One collection (*Black 52-15623*), listed separately in TABLE II as *Eugenia biflora* "B", differs considerably from the other four collections (see also TABLE II), viz.: Although the ovarian vasculature is of the FLORIDA-type (FIGURE 15), the pendulous placental strands are rather narrow, and there are very few connections between the dorsal bundles and other carpellary bundles. *Black 52-15623* also differs from the other collections in some less important respects: (1) Its staining properties are very different. (2) Much of the septum is often very thin, consisting of one to three layers of cells.

A second collection (*Schultes & Cabrera 14236*) is even more different and thus is also listed separately in TABLE II (as *Eugenia biflora* "C"). Differences from the other collections studied include the following: (1) Only four (as opposed to many) ovules are present per flower. (2) The number of major bundles is difficult to determine since these branch repeatedly throughout the floral tube. The relationship between the vasculature of the floral tube and that of the perianth parts is therefore ob-

scure. (3) Only one strand enters each sepal, but more than one supplies each petal. (4) The ovarian vasculature is quite unlike that of the other collections examined, but I cannot detail how it differs as my preparations are of poor quality. (5) The lateral carpellary system is only weakly developed, with apparently no anastomoses or connections to the dorsal bundles.

The three other collections (*Hart 1048*; *Pires & Westra 48813*; *Steyermark & Wurdack 31*), designated *Eugenia biflora* "A", are very similar, particularly in their vasculature. The entry *E. biflora* "A" in TABLE II is based on *Pires & Westra 48813*, which was studied in the greatest detail. These three collections differ chiefly as follows: (1) The maximum prolongation of the floral tube above the ovary was 0 mm. and .6 mm. for *Hart 1048* and *Steyermark & Wurdack 31*, respectively. (2) In *Pires & Westra 48813* usually only the two dorsal carpellary bundles continue to the tip of the style, but in the other two collections the two dorsals are often accompanied into the style by additional carpellary bundles.

Ranging from southern Mexico and the West Indies to Bolivia and northern Brazil (McVaugh, 1963b, 1969), *Eugenia biflora* is "probably the most widespread, and certainly the most variable, of any native [American] species of the family" (McVaugh, 1969, p. 167; see also McVaugh, 1958). The four South American collections I examined (see TABLE I) are cited under *E. biflora* by McVaugh (1969) in his most recent work on the Myrtaceae. At my request, McVaugh reexamined (August, 1971) the collections designated here as *E. biflora* "B" and "C", but he still thinks they are good *E. biflora*. In view of the notorious variability of this species, it is not surprising that *E. biflora* "A", "B", and "C" differ markedly (see TABLE II, which does not do justice to the differences between "A", "B", and "C"). However, perhaps these differences are no more significant than those evident between *E. salamensis* varieties *salamensis* and *hiraefolia* (see TABLE II).

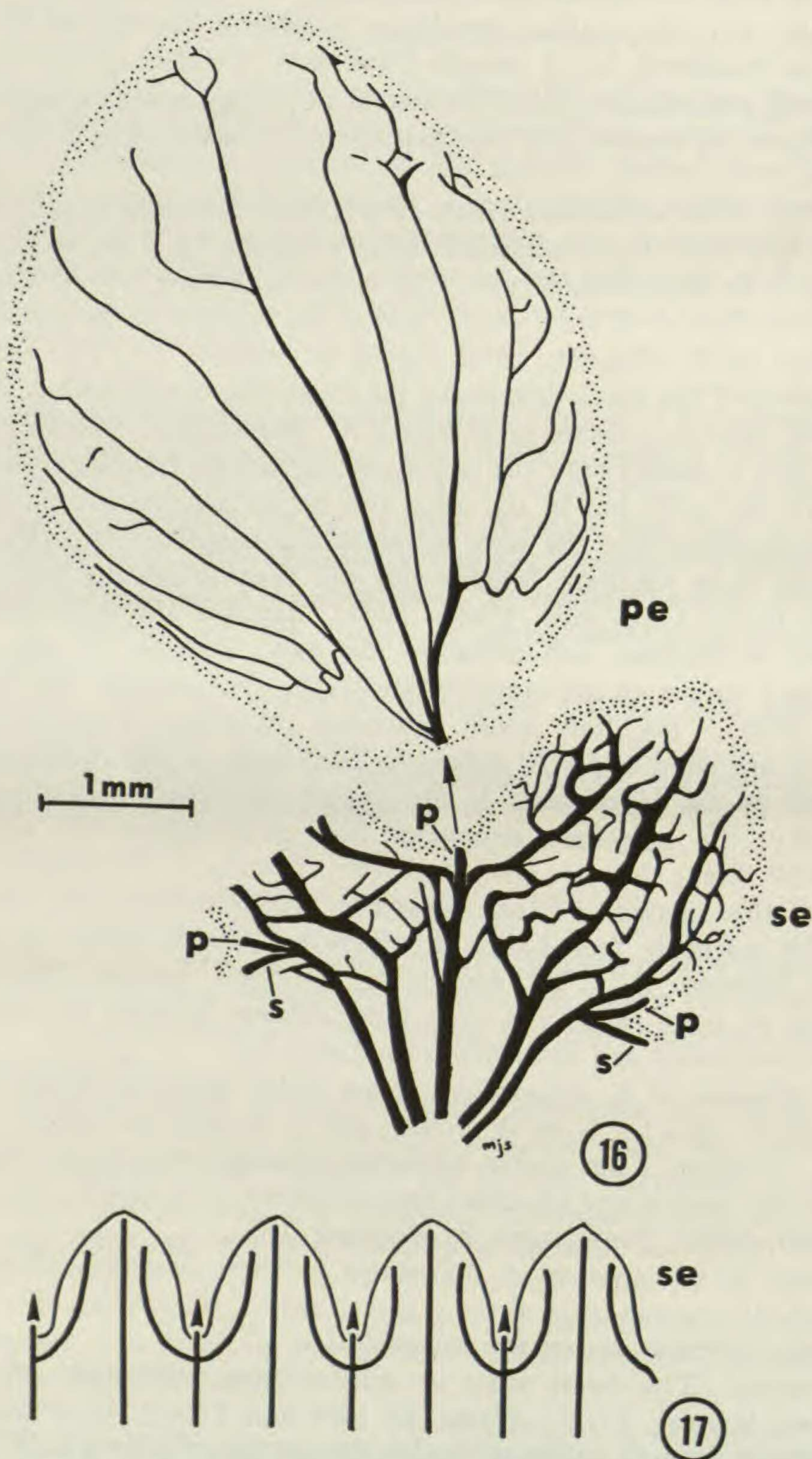
One collection of *E. biflora* "A" (*Hart 1048*) had been determined as var. *wallenii* (Macf.) Krug & Urban, and it is cited as such in Urban (1895). However, I am unable to see any clearcut anatomical differences between this variety and the other two collections of *E. biflora* "A" (*Pires & Westra 48813*; *Steyermark & Wurdack 31*).

In view of the anatomical differences between *Eugenia biflora* "A", "B", and "C", but in spite of the organographical similarities, this species apparently deserves taxonomic reappraisal.

HISTOLOGY. The dense silky or silky-strigose pubescence of simple hairs (see Schmid, 1972b, *Figure 12*, also like *Figure 9*) covering the floral tube and sepals is distinctive for this species (McVaugh, 1969).

VASCULATURE. The following description, based primarily on *Pires & Westra 48813*, pertains mainly to *Eugenia biflora* "A" and "B". For variations see above discussion and also TABLE II.

A single trace (several in *Steyermark & Wurdack 31*) supplies each bracteole. The vasculature of the floral tube and style is like that of *Eu-*



FIGURES 16, 17. *Eugenia biflora* (Pires & Westra 48813, MICH). FIGURE 16, Reconstruction of vasculature to and in three perianth parts; vasculature is complete. Only major vasculature indicated for most of floral tube. Vasculature to stamens and ovary omitted. FIGURE 17, Diagrammatic representation of major vasculature to perianth parts. Arrows indicate insertion of petals. ABBREVIATIONS: p, petal bundle; pe, petal; s, sepal bundle; se, sepal.

genia confusa (see TABLE II). However, as in several other species of *Eugenia s. s.* (e.g., *E. florida*, *E. oerstediana*, *E. uniflora*), in *E. biflora* there is a very regular relationship between the major bundles of the floral tube and the vasculature of the perianth parts (FIGURE 17). Eight major bundles, four sepal bundles alternating with four petal bundles, occur throughout the floral tube and produce many small minor, anastomosing strands (FIGURE 16). Distally, the four sepal bundles continue up the middle of the four sepals (FIGURES 16, 17). In contrast, each of the four petal bundles trichotomizes (FIGURES 16, 17), one of the three bundles that results entering each petal, the other two (lateral) bundles functioning as laterals of the two adjacent sepals. The bundle entering each petal branches profusely (FIGURE 16). The medial and two lateral bundles in each sepal anastomose extensively (FIGURE 16). A variable number of smaller bundles also enter the sepals (FIGURE 16).

The ovarian vasculature is of the FLORIDA-type (FIGURE 15), but exhibits considerable variability, even in the same plant. The lateral carpellary system, which is not very extensive, fuses with the dorsal bundles near the tops of the loculi. Two massive placental strands descend from points just above the loculi and terminate at a single placental plexus perforated by much parenchyma. The placental strands originate in a variety of ways, in some flowers mainly or exclusively from the two dorsal carpellary bundles. In addition slender placental strands frequently enter from the sides of the septum.

The dorsal bundles, which do not branch, originate at various levels, usually in the locular region, but often even near the base of the flower.

Eugenia coffeifolia DC.

See McVaugh (1969) and Urban (1895) for synonymy. Data were compiled mostly from the plant from St. Lucia since my preparations of the other collection were of poor quality. As far as I could tell, however, the two collections are very similar.

ORGANOGRAPHY and HISTOLOGY. The presence of only two ovules per locule is unusual in *Eugenia s. l.* (McVaugh, 1969), although as few as two or three ovules per locule also do occur in *E. oerstediana* (McVaugh, 1963a, b). The floral tube is strigose, with hairs similar to those in Figure 7 in Schmid (1972b). The style is sparingly pilose.

VASCULATURE: See TABLE II. The ovarian vasculature is of the FLORIDA-type (FIGURE 15). Near the tops of the loculi a variable number of strands of the anastomosing lateral carpellary bundles, often along with strands derived from the dorsal carpellary bundles, fuse into two large placental strands, which terminate at a single placental plexus containing little or no interfascicular parenchyma. Occasionally, additional, slender placental strands enter the septum via its sides and fuse with the placental plexus. The vasculature of the other floral parts resembles that of *Eugenia capuli* (see TABLE II).

Eugenia salamensis Donn. Sm.

Synonyms include *Psidium rensonianum* Standl., *Eugenia mexiae* Standl., and *E. hiraefolia* Standl. (see McVaugh, 1963a, b). I examined material of var. *salamensis* (this labelled *E. mexiae*) and var. *hiraefolia* (Standl.) McV. Unless otherwise noted, the following comments apply to both varieties.

Although both varieties are "readily distinguished" on the basis of vegetative characters in particular, McVaugh (1963a, p. 457) considered them "surely conspecific." Although it is a matter of taxonomic opinion, there seem sufficient anatomical differences between the two varieties, as noted below, that both could deservedly be retained as separate species, particularly if such very (and even more) similar taxa as *Eugenia capuli* and *E. venezuelensis* (see TABLE II) are regarded as distinct.

ORGANOGRAPHY and HISTOLOGY. Dibrachiate trichomes (see Schmid, 1972b, *Figure 13*) with short to long, equal or unequal, often contorted arms are very abundant on the floral tube and sepals. Variety *hiraefolia* was very tanniferous, var. *salamensis* only slightly so. The floral tube of the former is much more prolonged above the ovary than that of the latter (ca. 1.1 mm. maximum versus 0.2 mm. maximum, respectively). The only floral difference that McVaugh (1963a) noted for the two varieties was the slightly longer styles of var. *salamensis*. In buds, styles of var. *salamensis* are therefore doubled back whereas those of var. *hiraefolia* are erect or nearly so.

VASCULATURE. See TABLE II. The ovarian vasculature of var. *salamensis* was studied in much more detail, but that of var. *hiraefolia* seemed similar. The ovarian vasculature is of the FLORIDA-type (FIGURE 15). An anastomosing lateral carpellary system produces, usually just above the tops of the loculi, two massive placental strands that descend to the placental region. In addition, several slender placental strands frequently enter the sides of the septum.

The vasculature of the floral tube and style of var. *hiraefolia* is, respectively, like that of *Eugenia florida* and *E. venezuelensis* whereas that of var. *salamensis* is like that of *E. confusa* (see TABLE II). Differences in vasculature between the two varieties include characters 8, 10, 18, and 20 in TABLE II. Variety *hiraefolia* is much more heavily vascularized than var. *salamensis* and has many small anastomosing strands distributed between the loculi and the vascular cylinder of the floral tube.

Eugenia flavescens DC.

See McVaugh (1969) for synonymy.

HISTOLOGY. This is the only American species of *Eugenia s. l.* I studied that lacked secretory cavities in the anthers.

VASCULATURE. See TABLE II. The ovarian vasculature exemplifies the FLAVESCENS-type (FIGURE 18). An extensive lateral carpellary system consisting of slender anastomosing bundles girdles the loculi. From few

to many (up to about 11 per flower) placental strands depart from this lateral carpellary system, enter the septum, where they frequently anastomose, and terminate at the placental plexus (FIGURE 18). The dorsal carpellary bundles are connected to the lateral carpellary system at a number of points. Other features of floral vasculature resemble those of *Eugenia confusa* (see TABLE II).

Eugenia cartagensis Berg

HISTOLOGY. Phloem fibers occur throughout the pedicel, sclereids chiefly distally.

VASCULATURE. See TABLE II. The ovarian vasculature is of the FLAVESCENS-type (FIGURE 18). There are usually few placental strands, and in the septum these often fuse for a considerable extent. Bundles of the lateral carpellary system, which is not very extensive, anastomose chiefly near the tops of the loculi. The lateral and dorsal carpellary bundles are interconnected only at the tops of the loculi. Other features of floral vasculature are very much like those of *Eugenia confusa* or *E. flavescens* (see TABLE II) except that ten major bundles occur in some flowers of *E. cartagensis*.

Eugenia winzerlingii Standl.

One collection (*Lundell 851*) was analyzed most thoroughly. The three collections examined, however, are anatomically similar.

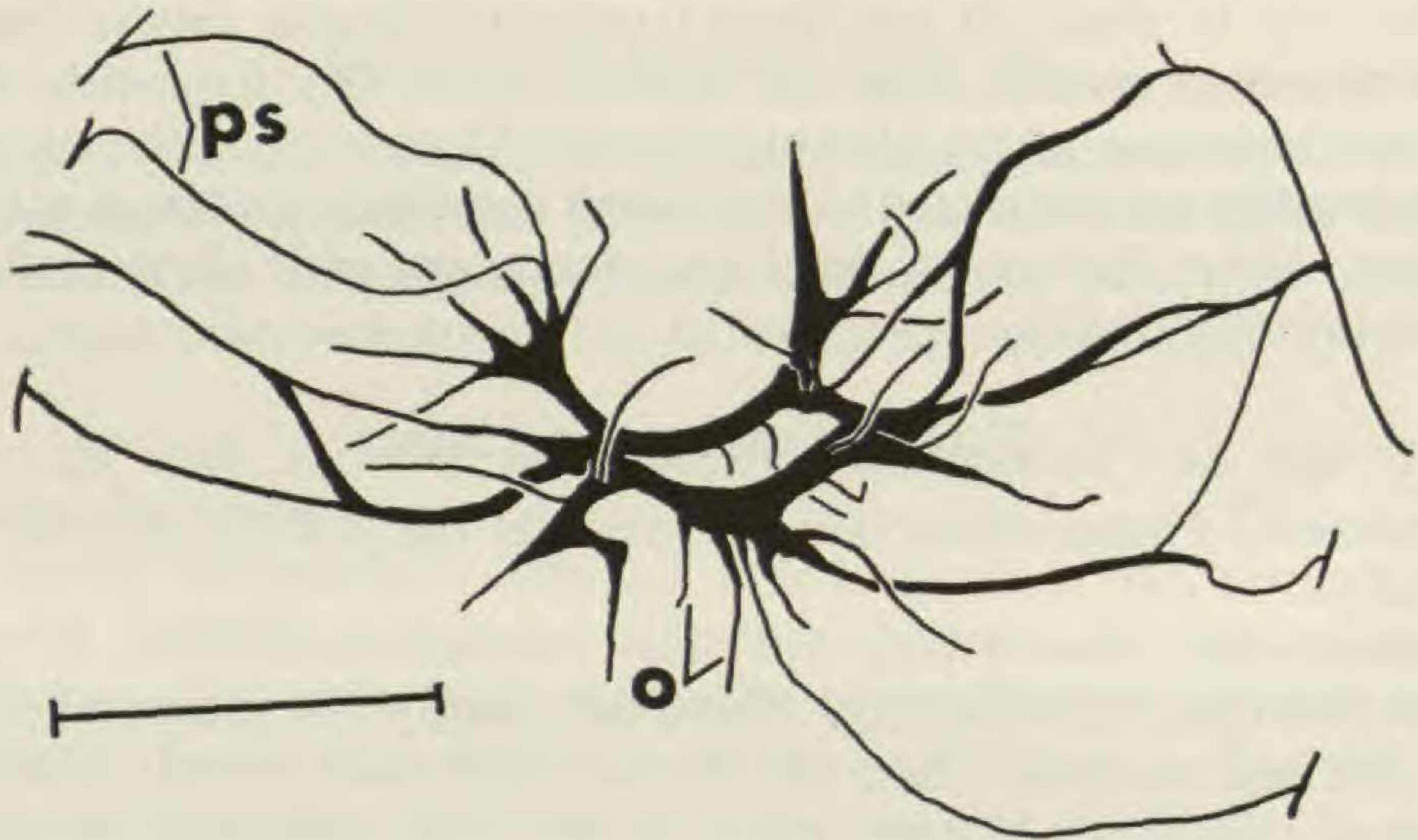
ORGANOGRAPHY and HISTOLOGY. The flowers are borne on filiform pedicels up to 20 mm. long (McVaugh, 1963b). The pedicels contain numerous narrow thin-walled phloem fibers commonly .4 to .5 mm. and often up to about .8 mm. long. One of the 14 flowers examined was tri-carpellate; its placental vasculature was similar to that of the other flowers. Unlike other species I studied, the walls of the loculi of *Eugenia winzerlingii* are lobate.

VASCULATURE. See TABLE II. The ovarian vasculature is of the FLAVESCENS-type (FIGURE 18.) However, the following differences from *Eugenia flavescens* were noted: The lateral carpellary system is less extensive. Two separate placental strands, as in *E. confusa* (FIGURES 1, 3), are present. Placental strands occasionally originate directly from the dorsal carpellary bundles.

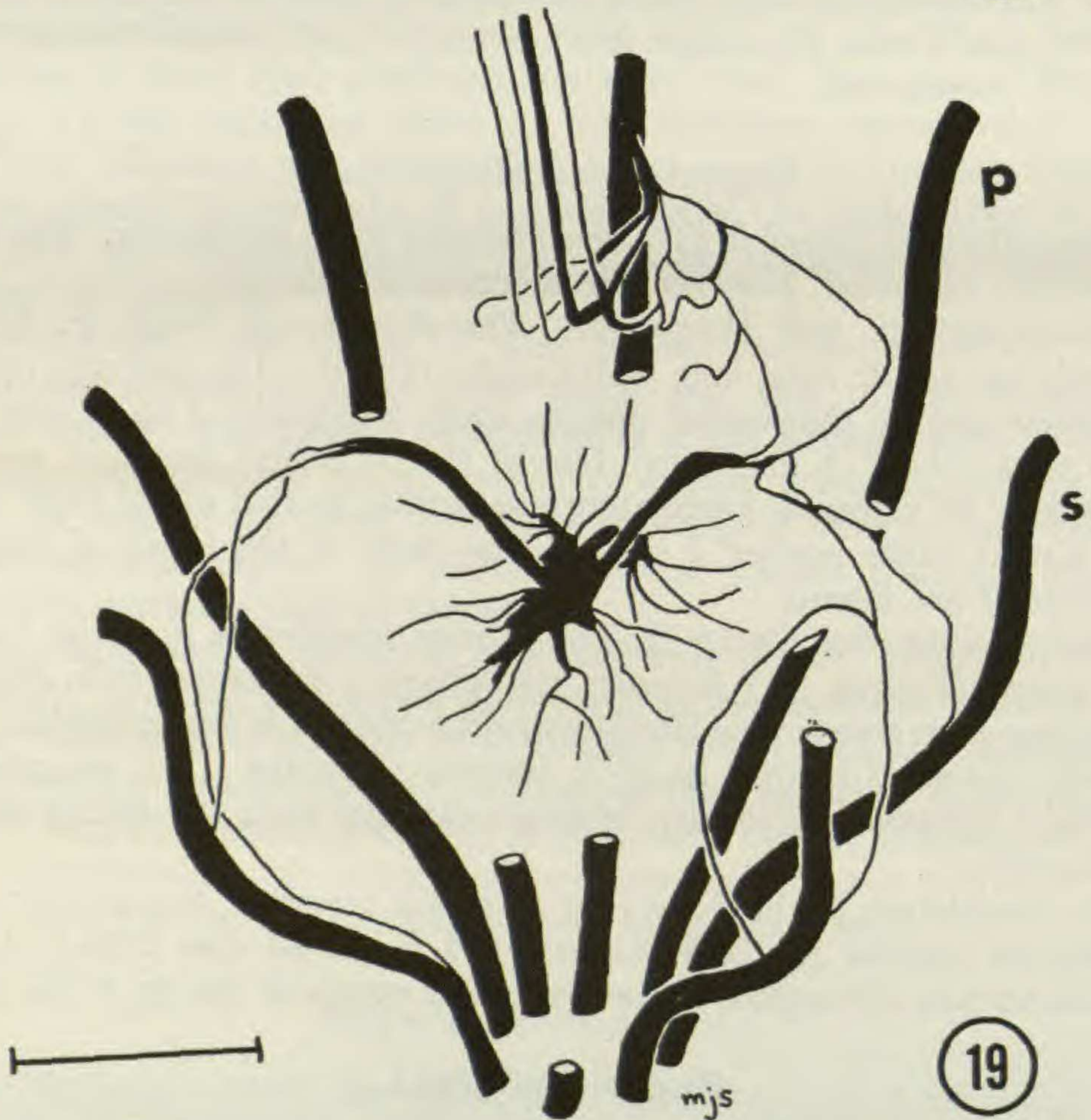
The vasculature of the floral tube and style resemble, respectively, that of *Eugenia confusa* (or *E. flavescens*) and *E. florida* (see TABLE II). A continuous ring of vascular tissue frequently occurs at the tip of the style.

Eugenia uniflora L.

Synonyms include *Myrtus braziliana* L., *Plinia rubra* L., *P. pedunculata* L. f., *Eugenia michelii* Lam., *Stenocalyx michelii* (Lam.) Berg, and *Eugenia decidua* Merr. [also "Myrtus indica" Tilli (1723); "Eugenia indica" Mich. (1729)] (see Berg, 1855-56; McVaugh, 1963b, 1969; Merrill, 1950; Urban, 1895). The two collections studied are similar.



18



19

FIGURES 18 and 19. FIGURE 18, *Eugenia flavescens*. Reconstruction of placental system showing placental strands traversing septum and terminating at a placental plexus. FIGURE 19, *Eugenia uniflora* (Taylor 48-1048, MICH). Reconstruction of cleared flower showing eight major bundles of floral tube, placental vasculature, and half of the carpellary vasculature destined for style.

Eugenia uniflora L., the type of *Eugenia* Linnaeus (1753),¹ is a cultigen commonly known as pitanga, Brazil cherry, Cayenne cherry, Florida cherry, or Surinam cherry. This species is one of the very few native American species of *Eugenia s. l.* to have been studied anatomically (see Petit, 1908, for the histology of seed and fruit).

ORGANOGRAPHY and HISTOLOGY. The filiform pedicels (up to 18 mm. long, McVaugh, 1963b) contain long narrow phloem fibers, as in *Eugenia winzerlingii*. Most flowers of *E. uniflora* are entirely glabrous, but one collection (Proctor 19469) I examined has a hairy staminal disc (with hairs as in Schmid, 1972b, Figure 6, excluding the hair on extreme left of figure).

The floral tube is conspicuously eight-angled, with a large (up to 70 μ in radial dimension) major bundle opposite each rib. The loculi are very large in relation to the rather narrow walls of the inferior ovary. *Eugenia pleurocarpa*, with a slightly eight-angled floral tube, is the only other species of *Eugenia s. l.* (31 studied in all, Schmid, 1971, 1972a-c) to have either of these characters. The fruit of *E. uniflora* is also prominently eight-costate.

VASCULATURE. See TABLE II. The vasculature of the floral tube is similar to that of *Eugenia biflora* (see TABLE II, FIGURES 16, 17). However, other features of vasculature of *E. uniflora* are quite distinctive, particularly the ovarian vasculature, which exemplifies the UNIFLORA-type (FIGURE 19). Several placental strands originate from various sources and at various levels in the floral tube (FIGURE 19), much as in *E. confusa* (FIGURE 1). On entering the septum, the placental strands usually fuse into two large compound placental strands. These turn downward as they traverse the septum and then terminate at a single placental plexus usually consisting of a solid mass of vascular tissue (FIGURE 19).

Unlike the species of *Eugenia s. s.* previously described, discrete dorsal carpellary bundles are not readily definable. Usually two large bundles originate in the positions where the dorsals would ordinarily be expected. These bundles, however, each quickly split into several fine, anastomosing strands (FIGURE 19), most of which eventually continue into the style. Occasionally, other carpellary bundles also supply the style. There are frequent connections between the placental vasculature and the strands supplying the style (FIGURE 19). The many styler bundles (as many as 12 in the base of the style) occasionally branch and often form a continuous ring of vascular tissue at the styler apex. A comparable situation occurs in certain species of *Alangium* (Eyde, 1968), but here, in contrast to *E. uniflora*, the two groups of fine, anastomosing strands taking the

¹ Authorities and dates of publication of genera follow the *Index Nominum Generi-corum*, which should be consulted for details.

place of the dorsals each fuse, forming a pair of well defined bundles that traverse the style.

OTHER TAXA WITH TRANSEPTAL OVULAR SYSTEMS

All the species of *Eugenia s. s.* listed below have transeptal ovular systems. In addition, all taxa have closed vascular systems, with the usually eight major bundles of the floral tube exhibiting a monocyclic arrangement. Vascular tissue extends to the apex of the style. The flowers lack sclerenchyma. However, the precise nature of these and other characters was not determined for these species for several reasons, in part because my clearings and many of my sections were of poor quality, and also because most of the buds of these species are very large and have extensive vascular tissue. A few distinctive features, chiefly of pubescence, are noted below.

(1) *Eugenia acapulcensis* Steud. See McVaugh (1963a, b) for synonymy. My material is glabrous, except for a slightly hairy staminal disc (with hairs like those in Schmid, 1972b, *Figure 5*).

(2) *Eugenia aeruginea* DC. Synonyms include *E. jadyenii* Krug & Urban ex Urban (see McVaugh, 1963b). The floral tube and sepals have an appressed, dense pubescence of dibrachiate hairs (as in Schmid, 1972b, *Figure 11*).

(3) *Eugenia duchassaingiana* Berg. The sepals and floral tube are very pubescent, with hairs as in *Figure 7* in Schmid (1972b).

(4) *Eugenia gregii* (Sw.) Poir. Synonyms include *Myrtus gregii* Sw., *Greggia aromatica* Solander ex Gaertn., and *Eugenia sieberiana* DC. (see Urban, 1895). *Eugenia gregii* is the type of the segregate genus *Greggia* Solander ex J. Gaertner (1788). This species has very distinctive infundibuliform hairs (see Schmid, 1972b, *Figure 8*) that form a dense mat on the floral tube and abaxial surfaces of the perianth parts. Other than these unusual hairs, however, the species certainly does not have any feature that might justify acceptance of the segregate genus *Greggia*. Superficially, the ovarian vasculature is of the FLORIDA-type (FIGURE 15).

(5) *Eugenia mandevillensis* Urban. Only the staminal disc and style are hairy (see Schmid, 1972b, *Figure 9*).

The secretory cavities are so remarkable in their (a) size, (b) abundance, and (c) distribution that this species might well be called the "American clove" of *Eugenia s. s.* (a) Size: The secretory cavities are, on the average, larger than those of any other species of *Eugenia s. l.* I have seen, including those of clove (*Syzygium aromaticum*, see Schmid, 1972b, c). At about 350 microns in dimension, the largest cavities are comparable in size to the largest of *S. aromaticum* and *S. malaccense*. (b) Abundance: The secretory cavities of *E. mandevillensis* are more numerous than those of any other species of *Eugenia s. l.*, with the possible exception of clove. In many parts of the flower, which is about 8–

9 mm. long in bud, the secretory cavities are so numerous that they occur as chains separated only by a few layers of epithelial cells. (c) Distribution: As in clove, the secretory cavities in the floral tube and the top of the ovary of *E. mandevillensis* frequently occur in two and even three intermixed layers (compare with *Figures 48, 49, 55, 56*, in Schmid, 1972c). Many cavities occur in the anthers (up to about seven per anther), filaments, and style, again as in clove. Unlike those of any other species of *Eugenia s. l.*, however, the secretory cavities of *E. mandevillensis* also occur in the ovarian tissue adjacent to the loculi and below them.

(6) *Eugenia muricata* DC. See McVaugh (1969) for synonymy. Many appressed-ascending, silky hairs (see Schmid, 1972b, *Figure 7*, also as in *Figure 12*) cover the floral tube and sepals.

(7) *Eugenia pleurocarpa* Standl. The floral tube and sepals are tomentose, covered by a pubescence of dibrachiate to mostly simple hairs of variable morphology (see Schmid, 1972b, *Figures 10, 11*). The flowers are very tanniferous, much more so than any other species of *Eugenia s. s.* I studied. See also remarks under *Eugenia uniflora* above.

(8) *Jossinia aherniana* (C. B. Rob.) Merr. Synonyms include *Eugenia aherniana* C. B. Rob. and *E. melastomoides* Elm. (see Merrill, 1950). The simple to dibrachiate hairs are figured in Schmid (1972b, *Figure 6*).

For vasculature see TABLE II. The floral vasculature is similar to that of the species of *Eugenia s. s.* described above except, that the flowers of *Jossinia aherniana* seem much more heavily vascularized. The placental vasculature of this species, however, is supplied not only transeptally by strands from the periphery of the septum, as in the previously described species of *Eugenia s. s.*, but also by a few bundles entering from the base of the septum, somewhat as in *Syzygium s. l.* (see Schmid, 1972c). In sharp contrast to *Syzygium s. l.*, however, the characteristically massive axile strand is lacking. In all, the ovarian vasculature most closely resembles the FLAVESCENS-type (FIGURE 18).

(9-10) Only fruiting material of the following two species, both from the Old World, was available. Both taxa have closed vascular systems and about eight major bundles of the floral tube in a monocyclic arrangement. Considerable vascular tissue occurs in the floral tube. The staminal discs of both species are hairy, more or less as in *Figures 6 and 9* in Schmid (1972b). Sclerenchyma occurs only in the seeds of *Jossinia palumbis* but throughout the fruit of *Eugenia whytei*, which has both fibers and sclereids. The vascular supply to the ovules seems to be of the transeptal type, but this conclusion is based on the examination of large, mature, one-seeded fruits in which there had been considerable displacement and disruption of the septum.

(9) *Eugenia whytei* Sprague in Stapf. Chattaway (1959) conjectured that this might represent a species of *Jossinia* rather than *Eugenia*.

(10) *Jossinia palumbis* (Merr.) Diels. Synonyms include *Eugenia palumbis* Merr. (see Diels, 1921).

DISCUSSION AND CONCLUSIONS

The transeptal ovular supply, which was found in all 23 species studied, varies considerably in structure even between different flowers of the same plant. As discussed in Schmid (1972b), the nature of the vascular supply to the ovules — transeptal in the mainly New World genus *Eugenia s. s.* versus axile in the exclusively Old World genus *Syzygium s. l.* — is the most distinctive anatomical difference between these taxa. In addition, other evidence from both reproductive and vegetative anatomy and morphology also supports the fundamental disparity of these two taxa (Schmid, 1971, 1972b). While there seems to be convincing evidence that most Old World species of *Eugenia s. l.* are distinct from the New World ones (Schmid, 1971, 1972b), it is more difficult to differentiate, anatomically, between the various segregate genera of *Eugenia s. s.*²

Except for the taxa discussed below, most of the species of *Eugenia s. s.* I analyzed have never been placed in segregate genera. Consequently, my conclusions on the various species relationships seem more appropriately discussed above where the species are first described.

Eugenia gregii is the type species of the segregate genus *Greggia* Solander ex J. Gaertner (1788). However, only the authors who proposed it seem to have accepted this segregate. The floral anatomy of *E. gregii* is entirely consistent with its placement in *Eugenia s. s.*

Stenocalyx Berg (1856), characterized by precocious flowers, has also won little credibility among botanists. Bentham (1869) condemned the use of so vague and variable a feature, and nearly a hundred years later McVaugh (1968) concurred. However, Kausel (1957, 1966), the arch splitter of the Myrtaceae, still assesses *Stenocalyx* as valid. Anatomically, *Eugenia uniflora* (= *Stenocalyx michelii*), the type species of *Stenocalyx* (as well as of *Eugenia* Linnaeus, 1753), is certainly at home in *Eugenia s. s.* To be fair, however, this species is undeniably different in many respects from most other species of *Eugenia s. s.* (see TABLE II). In addition, Chattaway (1959) found *E. uniflora* to differ from the majority of the New World species in its bark structure. These differences, however, merely reinforce the notion that *E. uniflora* and its relatives occupy a somewhat isolated position within the genus. The anatomical differences do not justify generic status, however, since they merely conform to the great anatomical (and organographical) diversity of a very kaleidoscopic genus (see Schmid, 1972b). Actually, in view of the variation that *Eugenia s. s.* exhibits, I am not at all certain that *E. uniflora* and its relatives

² See McVaugh (1968) for an excellent discussion of the taxonomy of the American Myrtaceae, and also Kausel (1957), McVaugh (1968), and Niedenzu (1893) for generic synonymy of *Eugenia s. s.*

are even worthy of subgeneric rank, the status to which Niedenzu assigned them (1893) in his taxon *Macrocalyx*. Indeed, Bentham (1869) long before pointed out the great polymorphy of calyx structure in *Eugenia*, which became the basis for Niedenzu's characterization.

The floral anatomy of the Old World genus *Jossinia* Commerson ex De Candolle (1828) is very similar to that of the American species of *Eugenia s. s.* (see TABLE II), differing only in the nature of the vascular supply to the ovules. All the evidence from both vegetative and reproductive organography and anatomy now available (see Schmid, 1971) demonstrates that *Jossinia* is so very similar to the American species of *Eugenia s. s.* that segregation of *Jossinia* as a genus seems unwarranted. *Jossinia* may well represent a residue of Old World species of *Eugenia s. s.* that, in some of its taxa, exhibits a rather primitive transeptal ovular system, one perhaps transitional between the axile ovular system of the Old World *Syzygium s. l.* and the transeptal ovular system of the New World species of *Eugenia s. s.* (Schmid, 1971). These aspects will be elaborated in a subsequent publication in this series (Schmid, in preparation).

SUMMARY

There seems to be no anatomical basis for the recognition of the following generic segregates of *Eugenia s. s.*: *Greggia*, *Jossinia*, and *Stenocalyx*. *Stenocalyx* admittedly occupies a somewhat isolated position within *Eugenia s. s.*, but the differences of the former merely conform to the great organographical and anatomical diversity of a very kaleidoscopic genus. The organography and anatomy of the Old World *Jossinia* species are very similar to those of the American species of *Eugenia s. s.*

The following conclusions were drawn about the relationships of various species of *Eugenia s. s.* (1) *Eugenia capuli*, *E. tikalana*, and *E. venezuelensis* represent a complex of very closely related species. (2) *Eugenia florida* is best regarded as a widely distributed complex comprised of such scarcely distinguishable forms or varieties as *E. oerstediana*, *E. conzattii*, and *E. cocquericotensis*. (3) *Eugenia salamensis* varieties *salamensis* and *hiraefolia* seem sufficiently distinct so that at least varietal and probably specific status is justified. (4) *Eugenia biflora* was found to contain a number of anatomically different but organographically similar forms and deserves taxonomic reappraisal.

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